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Understorey plant community dynamics following a large, mixed severity wildfire in a *Pinus ponderosa*–*Pseudotsuga menziesii* forest, Colorado, USA

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Colorado Front Range; Douglas-fir; Fire severity; Hayman Fire; Ponderosa pine; Riparian areas; Time since fire

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Abstract

Question: How do understorey plant communities of *Pinus ponderosa–Pseudotsuga menziesii* forests respond during the first 5 yrs following wildfire, and do responses vary with fire severity?

Location: Colorado Front Range, USA.

Methods: In 2002, the Hayman Fire burned across 55 800 ha of Colorado Front Range *P. ponderosa–P. menziesii* forest. Also burned in the fire were 20 upland and five riparian plots within a 400-ha study area. These plots had been surveyed for understorey plant composition and cover 5–6 yrs prior. We re-measured all plots annually from 2003 to 2007, 1–5 yrs post-fire. Changes in the occurrence of common understorey plant species and in metrics of understorey plant richness and cover were analysed with regard to fire severity and time since fire using repeated measures ANOVA. Compositional changes were explored using ordination.

Results: Fire severity (defined in terms of overstorey mortality, overstorey canopy consumption, and forest floor consumption) in upland plots was highly variable, with 50%, 30% and 20% of plots burning with low, moderate and high severity, respectively. For all severities, total cover in uplands declined in the first post-fire year relative to pre-fire levels, but met or exceeded pre-fire levels by post-fire year five. Total richness in uplands, however, did not similarly decline immediately following fire, due largely to a high return rate of pre-fire species, and exceeded pre-fire levels for all severities from post-fire years 3–5 due to new species recruitment. Over 90% of the common upland species either were found in a similar number of plots before and after the fire, regardless of fire severity or time since fire, or were found in more plots following the fire in at least 1 yr and one severity class. Temporal changes in upland composition occurred for all severities but were most pronounced following moderate and severe fire. In contrast, riparian plots largely burned with low severity, and the understorey plant communities within them exhibited little change in richness, cover and composition over the 5 yrs.

Conclusions: Our results suggest that the Hayman Fire had largely neutral or stimulatory impacts on understorey plant communities following the first five post-fire years.

Introduction

Mixed severity fire events are key disturbance agents for many coniferous forest ecosystems (Arno 1980; Brown et al. 1999; Turner et al. 1999; Burton et al. 2008; Oliveras et al. 2009; Collins & Stephens 2010). Such fires are characterized by their high spatial variability in fire behaviour and immediate fire effects. When defined in terms of fire's direct impact on the dominant vegetation – trees – mixed severity fires create severely burned patches where all trees are killed and the canopy is largely consumed, as well as moderately or lightly burned patches where some or even all of the overstorey trees survive (Perry et al. 2011). Mixed severity fires typically also create diverse effects on the forest floor, with surface organic layers varying across the fire footprint from consumed to blackened to unburned (Groeschl et al. 1993; Parsons et al. 2010). Thus, mixed severity fires typically result in a complex mosaic of overstorey stand structures and forest floor conditions on the landscape.

Post-fire understorey plant community development following mixed severity fire is shaped both by fire severity patterns and by attributes of the species growing within and surrounding the burns (Schimmel & Granström 1996; Turner et al. 1997; Wang & Kemball 2005). Many coniferous forest understorey species are considered to be fire-adapted due to their ability to establish shortly following fire via sprouting or via on- or off-site seed sources (Rowe 1983). After low severity fire, understorey plants in these forests are often only minimally impacted because below-ground plant parts are not exposed to lethal temperatures, and overstorey densities and litter layers are not reduced enough to allow for significant new species establishment from seed (Kuddes-Fischer & Arthur 2002; Laughlin & Fulé 2008; Nelson et al. 2008). In contrast, understories in severely burned areas can be dramatically altered. Following severe fire, even sprouting species can be reduced in frequency or cover if the fire is hot enough to kill below-ground structures (Schimmel & Granström 1996; Turner et al. 1997; Doyle et al. 1998). The recruitment of new species is also a common phenomenon following severe fire (Doyle et al. 1998; Huisinga et al. 2005; Wang & Kemball 2005). Indeed, changes in understorey communities due to high severity fire can be long lasting, taking decades for understorey properties to return to pre-fire conditions, if at all (Halpern 1988; Savage & Mast 2005; Bataineh et al. 2006; Coop et al. 2010).

In Colorado Front Range forests dominated by *Pinus ponderosa* (ponderosa pine) and *Pseudotsuga menziesii* (Douglas-fir), tree-ring evidence suggest that historical fires were typically mixed in terms of severity, as well as in terms of other fire regime characteristics such as interval and extent (Brown et al.1999; Huckaby et al. 2001; Sherriff & Veblen 2006). These same data also show that wildfire occurrence was greatly reduced beginning in the early 20th century, due to fire suppression and other factors. However, Colorado Front Range *P. ponderosa – P. menziesii* forests have experienced a recent resurgence in wildfire occurrence (Litschert et al. 2012), with nearly 250 000 ha burned in the last two decades. Thus, there has been little opportunity until now to examine how understorey plant communities and other ecosystem properties are influenced by wildfire in these forests.

At over 55 800 ha, the 2002 Hayman Fire is the largest fire known to have occurred in Colorado to date (Graham 2003). This fire was ignited on the afternoon of June 8. Extremely low fuel moistures, heavy, continuous fuel loadings and strong, gusty winds allowed the Hayman Fire to burn over 24 000 ha on June 9, largely as a high severity fire with complete overstorey mortality (Finney et al. 2003). While dendrochronological studies conducted within the perimeter of the Hayman Fire suggest that historical fires often contained a significant high severity component, the size of the large high severity patches created by the Hayman on this day appears to be unprecedented over the last five centuries (Brown et al. 1999; Huckaby et al. 2001). Less extreme weather conditions followed the next day and more-or-less persisted for the following 3 wks, causing the fire to burn with a more heterogeneous mosaic of severities until it was contained on July 2 (Finney et al. 2003). Fire severity maps developed by the Hayman Burned Area Emergency Rehabilitation Team indicate that ca. 49% of the total fire footprint was unburned or burned with low severity, while 16% burned with moderate severity and 35% burned with high severity (Robichaud et al. 2003).

Pre-existing upland and riparian understorey plots within the Hayman perimeter have provided a unique reference condition for examining post-fire understorey plant community dynamics. These plots, which were initially established and measured in 1996 or 1997 (Kaufmann et al. 2000; Fornwalt et al. 2003, 2009), were re-measured annually from 2003 to 2007, 1–5 yrs post-fire. We utilized data collected in upland plots, which burned with a range of severities, to address the following three questions: (1) what were the impacts of fire severity and time since fire on common upland understorey species; (2) did total and functional group (short-lived forb, long-lived forb, graminoid and woody plant) understorey richness and cover change as a result of the fire, and did these changes vary with fire severity and over time; and (3) did the Hayman Fire have any immediate impact on understorey species composition across fire severity classes, and did pre-fire and post-fire communities within these classes become more similar or less similar as time passed? Utilizing data collected in riparian plots, where fire severity was generally low, we asked: (1) how were common riparian species impacted by fire; (2) how did total and functional group richness and cover vary as time since fire passed; and (3) did species composition change with time since fire?

Methods

Study area and study design

We conducted our study in a 400-ha portion of the Pike National Forest, Colorado, USA, ca. 60 km southwest of Denver. Forests here are dominated by *P. ponderosa* and *P. menziesii*, while understories are a diverse community of

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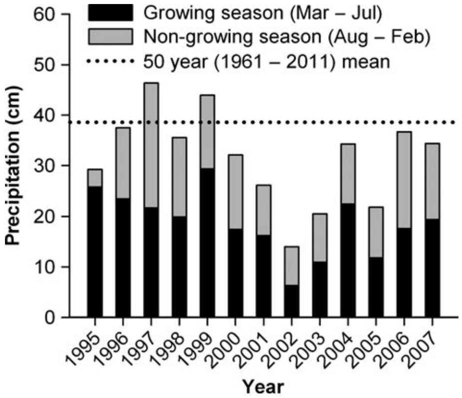

Fig. 1. Growing season (March through July) and non-growing season (August through February) precipitation for the years prior to and during this study. Data were collected at the Manitou Experimental Forest (http://www.fs.usda.gov/main/manitou/data/data-catalog), ~12 km from our study area. The Hayman Fire occurred in 2002. Sampling occurred pre-fire in 1996 or 1997, and post-fire in 2003, 2004, 2005, 2006 and 2007.

graminoids, forbs and shrubs (Kaufmann et al. 2000; Fornwalt et al. 2003, 2009). Soils on upland slopes are gravelly coarse sandy loams derived from weathered Pike's Peak granite; in drainage bottoms, soils are also of granitic origin but are generally finer and more developed (USDA Forest Service 1992). Study area elevations range from 2300 to 2500 m. Annual precipitation averages around 38 cm, although variation among years can be considerable (Fig. 1; http://www.fs.usda.gov/main/manitou/data/data-catalog).

The study area has a history of both natural and human disturbance. Fire history information collected in and around our study area suggests that, prior to Euro-American settlement in the late 19th century, fire intervals for individual stands varied from short (<10 yrs) to long (>100 yrs), and fire severity likewise varied from low severity surface fires to stand-replacing, high severity fires (Brown et al. 1999). A policy of fire suppression has been in place since the 1900s, and little of our study area has experienced wildfire since then (i.e. until the 2002 Hayman Fire). Logging and grazing from the 1880s to the 1900s were rampant, but these activities are not believed to have occurred since (DeLay 1989; Fornwalt et al. 2009).

The study area contains 25 1 000-m^2 (20 × 50 m) plots that were originally established and measured in 1996 or 1997 (Kaufmann et al. 2000; Fornwalt et al. 2003, 2009). Five plots were located in each of five topographic environments: north-facing slopes, south-facing slopes, east- or west-facing slopes, ridgetops and riparian areas. North, south, east/west and ridgetop plots were situated in upland areas, while riparian plots were located in low-lying valley bottoms or draws near intermittent or perennial streams.

In 2002, the study area burned in the Hayman Fire (Fig. 2). Situated in a transitional zone between the extreme fire behaviour observed on June 9 and the less extreme fire behaviour of the following weeks, it contains portions of large high severity patches, as well as smaller low, moderate and high severity patches (Robichaud et al. 2003). In 2003, we successfully relocated and re-measured all original plots. Plot locations were able to be accurately reconstructed from pre-fire data such as plot coordinates and overstorey stem maps, as well as from the remains of plot corner stakes and aluminium tree tags. Plots were also re-measured annually from 2004 to 2007.

Data collection

Direct fire effects on the overstorey and forest floor were assessed for each plot in 2003 (Table 1). Percentage overstorey mortality equalled the percentage of pre-fire live trees over 1.37-m tall (determined by Kaufmann et al. 2000 when the plots were established) that were dead in 2003. The percentage of the pre-fire crown volume that was scorched and consumed was visually estimated for each tree. We assessed fire effects on the forest floor by

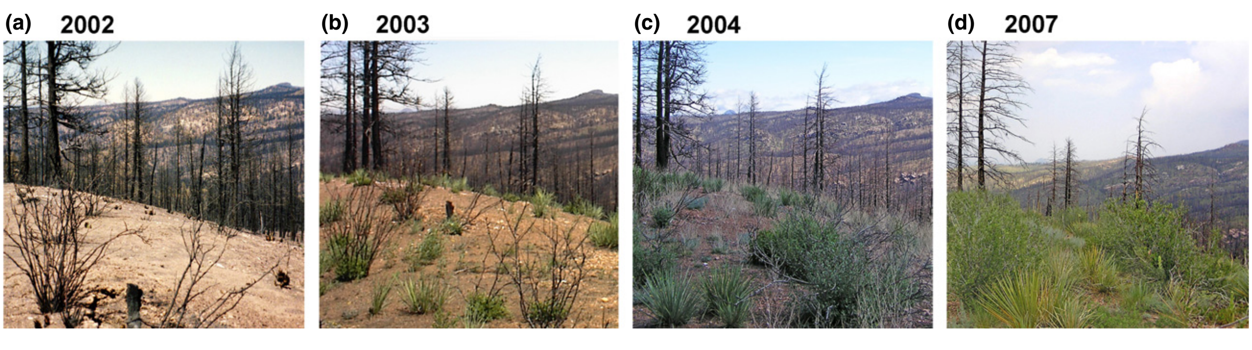

Fig. 2. Representative example of changes in the forest understorey following the 2002 Hayman Fire. Photographs were taken on a severely burned ridgetop within the 400-ha study area. The post-fire recovery of *Cercocarpus montanus* (alderleaf mountain mahogany) and *Yucca glauca* (soapweed yucca) is particularly apparent in this photo series. 2002 photo by M. Kaufmann; all other photos by P. Fornwalt.

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Table 1. Direct effects of the 2002 Hayman Fire on the overstorey and forest floor, by topographic category and fire severity. All measurements were made in 2003. Values are means ± SE. Litter, small wood and large wood characteristics are for pre-fire material; freshly fallen material was disregarded.

	Upland			Riparian
	Low severity (n = 10)	Moderate severity (n = 6)	High severity (n = 4)	Low severity (n = 4)
Overstorey				
Mortality (%)	21 ± 4	67 ± 4	100 ± 0	33 ± 6
Crown scorch (%)	36 ± 6	37 ± 3	1 ± 1	42 ± 4
Crown consumption (%)	10 ± 3	50 ± 4	99 ± 1	8 ± 2
Total crown damage (%)	46 ± 7	87 ± 3	100 ± 0	50 ± 7
Forest floor				
Litter characteristics	Partially to fully blackened, partially consumed	Partially consumed	Largely consumed	Partially to fully blackened, partially consumed
Small Wood (<7.6 cm) characteristics	Partially to fully blackened, rarely consumed	Partially consumed	Largely consumed	Partially to fully blackened, rarely consumed
Large Wood (>7.6 cm) characteristics	Partially blackened	Partially consumed	Partially consumed	Partially blackened

noting the condition (unburned, partially blackened, fully blackened, partially consumed and fully consumed) of pre-fire litter, small wood and large wood in ten 1-m^2 subplots; freshly fallen litter and wood were disregarded.

Pre-fire and post-fire understorey composition and cover data were collected for each plot using the modified Whittaker sampling design (Stohlgren et al. 1995). In this design, vegetative cover is visually estimated for each understorey plant species in ten 1-m^2 subplots, while species presence is recorded for two 10-m^2 subplots, one 100-m^2 subplot and the larger 1000-m^2 plot. All graminoid, forb and shrub species were included in our understorey surveys, but tree species were not. While most identifications were made to species, in some instances identifications were made only to genus if species were difficult to distinguish when sampled outside peak morphological development (hereafter these identifications are also referred to as species). Voucher specimens are stored at the USDA Forest Service Rocky Mountain Research Station in Fort Collins, Colorado.

Data analyses

To aid in analyses, plots were first classified into groups reflecting their fire severity and topographic position. Fire severity was classified as low, moderate or high based on the fire's direct effects on the overstorey and forest floor. Plots where less than 50% of the overstorey trees died in the fire were categorized as burning with low severity, while moderate severity plots experienced 50% overstorey mortality or more but had only modest levels of crown and forest floor consumption. High severity plots were those with 100% tree mortality and complete or nearly complete crown and forest floor consumption. Based on the plot's pre-fire topographic environment designation, topographic position was defined as either upland (i.e. north, south, east-west and ridgetop topographic environments) or riparian. Previous work in these plots found few differences in pre-fire understorey community characteristics among upland plots, although upland and riparian plots differed considerably (Fornwalt et al. 2003, 2009). Using this classification scheme, our data set contains ten low, six moderate and four high severity upland plots. The four upland topographic environments were relatively well distributed with respect to fire severity, with each fire severity class containing at least three of the four environments. Our data set also contains four low, one moderate and no high severity riparian plots. The moderate and high severity riparian classes are not included in subsequent analyses because they are not sufficiently replicated. Post-fire rehabilitation treatment maps developed by the Burned Area Emergency Rehabilitation Team indicate that four plots were aerially seeded with exotic annual cereal grasses in the autumn of 2002 (Robichaud et al. 2003). Seeded grasses were most abundant in the plots in 2003, but even in this year seeded grass cover was <1%. Owing to this negligible cover, we did not distinguish seeded from unseeded plots.

Species were classified in two ways. First, species were classified as either 'legacy' species or 'new' species. Legacy species were those found during a plot's pre-fire survey, while new species were found in a plot only after the fire. A species could be a legacy species in one plot but a new species in another, depending on whether or not it was recorded before the fire. Species were also classified into one of four functional groups based on life history and growth form characteristics; these functional groups included short-lived forbs (i.e. annuals and biennials), long-lived forbs (i.e. perennials), graminoids and woody plants (i.e. shrubs and sub-shrubs). Short- and long-lived graminoids were not separated into their own categories because short-lived graminoids were scarce. Classifications

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were made using the USDA Plants Database (http://www.plants.usda.gov) and local botanical keys (Harrington 1964; Weber & Wittmann 2001).

Fire impacts on individual understorey species were examined using repeated measures ANOVA in SAS 9.1.3 (GLIMMIX procedure; SAS Institute Inc., Cary, NC, US). These analyses were conducted in place of the often-used indicator species analysis (ISA; Dufrêne & Legendre 1997), which was not appropriate because ISA cannot account for correlations among repeated observations. To limit the number of analyses conducted, only the most common species – i.e. those species occurring in more than 75% of the upland or riparian plots in at least 1 yr – were examined. For upland plots, we modelled species presence/absence in the 1000-m^2 plots against the factors year, fire severity and year × fire severity. For riparian plots, where only low severity plots were available for analysis, we modelled species presence/absence against the factor year. All analyses used the spatial power covariance matrix, which assumes that there is a higher level of correlation between two repeated observations closer in time than between two observations further apart. When year or year × fire severity was significant, pair-wise differences between years were further examined using least squares means with a Tukey–Kramer adjustment for multiple comparisons. Significance was assessed using $\alpha = 0.05$.

Fire impacts on measures of richness and cover were similarly examined using repeated measures ANOVA. Total richness was calculated by tallying the number of species per 1000-m^2 plot. Total cover was calculated by summing the cover of all species in each 1-m^2 subplot and averaging across the ten subplots per plot. Richness and cover for legacy species, new species and for species within each of the four functional groups were calculated in a similar manner. Cover data were square-root transformed prior to analysis to improve the distribution and homogeneity of residuals. Analyses of upland data were conducted by modelling each richness and cover measure against year, fire severity and year × fire severity, while analyses of riparian data were conducted by modelling measures against year.

Compositional differences among years and fire severities were investigated using the non-metric multi-dimensional scaling (NMS) ordination procedure in PC-ORD 5.0 (McCune & Grace 2002). The following procedure was conducted separately for upland and riparian plots, using species presence/absence data for the 1000-m^2 plots. First, we assessed the dimensionality of the data set by running 250 preliminary ordinations using a step-down in dimensionality procedure (i.e. one- through six-dimensional solutions were calculated for each of the 250 runs) and a random starting configuration. Each run used the Sørensen distance measure to calculate the distance matrix, a maximum of 500 iterations, and a stability criterion of 0.00001. The optimal preliminary ordination was the one whose configuration minimized the number of dimensions in the solution while also minimizing stress, and where the Monte Carlo *P*-value from 250 runs with randomized data was less than 0.05. Next, we conducted a final ordination run with the optimal preliminary ordination configuration used as the starting configuration. The final ordination was then rigidly rotated to align year with axis 1.

Results

A total of 247 understorey plant species were found across all 24 plots (excluding the single moderate severity riparian plot) and all 6 yrs. Of these, 23% were short-lived forbs, 48% were long-lived forbs, 16% were graminoids, 9% were woody plants and 4% were genus-only identifications that could not be classified into functional groups due to variability within the genus. Exotics were a relatively minor component of the understorey before and after the Hayman Fire, accounting for 8.5% of all understorey species found; a detailed analysis of post-fire exotic response can be found in our previous work (Fornwalt et al. 2010).

Species-level responses to fire in uplands

A total of 42 common species were identified for upland plots and were analysed to examine their individual response to the Hayman Fire (Table 2). Fire-induced changes in species presence/absence were readily apparent among the common short-lived forbs, while common long-lived forbs, graminoids and woody plants were much less responsive. Ten of the 13 common short-lived forbs examined here were more frequently encountered after the fire than before for one or more post-fire years, with the duration of the post-fire increase for several species lengthening as fire severity increased [e.g. the native species *Conyza canadensis* (Canadian horseweed) and the exotic species *Verbascum thapsus* (common mullein)]. In contrast, 16 of the 21 common long-lived forb species, four of the five common graminoid species and two of the three common woody plant species consistently occurred in a similar number of plots pre-fire and post-fire. Only one common species, the woody plant *Arctostaphylos uva-ursi* (kinnikinnick), was less frequently encountered following the fire for all five post-fire years, although this decline was limited to severely burned areas.

Post-fire richness and cover in upland forests

Total understorey richness in upland plots varied with year and with the interaction between year and fire severity,

Table 2. Changes in the presence/absence of common upland understorey species between pre-Hayman (1996–7) and post-Hayman (2003–7) sampling periods. Fire severity impacts are shown only if year × fire severity was significant in the ANOVA. '–' indicates that the number of post-fire plots containing that species was similar to pre-fire values for that year, while '↑' and '↓' indicate that the number of post-fire plots increased/declined relative to pre-fire values. Species that were found in a similar number of pre-fire and post-fire plots for all five post-fire years are listed below the table [a].

Species	Fire Severity	Response to the Hayman Fire				
		2003	2004	2005	2006	2007
Short-Lived forbs						
Bahia dissecta		–	↑	↑	↑	↑
Chenopodium spp.		↑	↑	↑	↑	↑
Conyza canadensis	Low	–	–	–	–	↑
	Mod	↑	–	↑	↑	↑
	High	–	–	↑	↑	↑
Corydalis aurea		↑	↑	–	↑	–
Lactuca serriola [b]	Low	↑	–	–	–	↑
	Mod	↑	–	↑	↑	↑
	High	–	–	↑	↑	↑
Laennecia schiedeana		–	–	↑	–	↑
Machaeranthera bigelovii		–	–	↑	↑	↑
Phacelia heterophylla		↑	↑	↑	↑	↑
Tragopogon dubius [b]	Low	–	–	–	–	↑
	Mod	↑	–	↑	–	↑
	High	–	–	↑	↑	↑
Verbascum thapsus [b]	Low	–	–	↑	–	↑
	Mod	↑	↑	↑	↑	↑
	High	–	↑	↑	↑	↑
Long-Lived Forbs						
Achillea millefolium	Low	–	–	–	–	–
	Mod	–	–	–	–	–
	High	↓	↓	–	–	–
Artemisia frigida		–	–	–	–	↑
Erigeron compositus		↓	–	–	–	–
Penstemon glaber		–	↑	↑	↑	↑
Taraxacum officinale [b]		–	–	–	↑	↑
Graminoids						
Muhlenbergia montana	Low	–	–	–	–	–
	Mod	–	–	–	–	–
	High	↓	–	–	–	–
Woody Plants						
Arctostaphylos uva-ursi	Low	–	–	–	–	–
	Mod	–	–	–	–	–
	High	↓	↓	↓	↓	↓

[a]Common upland understorey species that were consistently found in a similar number of pre-fire and post-fire plots: short-lived forbs — *Androsace septentrionalis*, *Artemisia campestris* and *Erysimum capitatum*; long-lived forbs — *Allium cernuum*, *Antennaria parvifolia*, *Arabis fendleri*, *Artemisia ludoviciana*, *Geranium caespitosum*, *Heterotheca villosa*, *Mertensia lanceolata*, *Noccaea montana*, *Packera fendleri*, *Penstemon secundiflorus*, *Penstemon virens*, *Potentilla fissa*, *Pulsatilla patens*, *Sedum lanceolatum*, *Solidago* spp. and *Yucca glauca*; graminoids — *Carex* spp., *Koeleria macrantha*, *Poa fendleriana* and *Schizachyrium scoparium*; and woody plants — *Cercocarpus montanus* and *Ribes cereum*.

[b]Exotic to the continental United States.

Table 3. ANOVA results for the effects of year, fire severity and year × fire severity on measures of understorey richness and cover in upland plots. Significant ($P < 0.05$) are shown in bold.

Understorey Response	Year (P-value)	Fire Severity (P-value)	Year × Fire Severity (P-value)
Total Richness (1000 m^2)	**<0.001**	0.079	**0.014**
Legacy/New Richness (1000 m^2)			
Legacy Species	0.146	**0.010**	0.400
New Species	**0.011**	**<0.001**	**0.004**
Functional Group Richness (1000 m^2)			
Short-Lived Forbs	**<0.001**	0.856	**<0.001**
Long-Lived Forbs	**<0.001**	**0.010**	0.276
Graminoids	**0.017**	0.406	0.278
Woody Plants	0.283	0.611	0.525
Total Cover (%)	**<0.001**	0.410	**0.008**
Functional Group Cover (%)			
Short-Lived Forbs	**<0.001**	**0.010**	**<0.001**
Long-Lived Forbs	**<0.001**	0.497	0.137
Graminoids	**<0.001**	0.564	0.093
Woody Plants	**<0.001**	0.460	0.448

but not with fire severity *per se* (Table 3, Fig. 3). For all fire severities, pre-fire and post-fire total species richness was similar for the first one to two post-fire years. Total richness subsequently increased in post-fire years 3–5.

On average, 31 of the species originally found in each plot before the fire – 80% of total pre-fire richness – were legacy species that were also found during post-fire surveys in any given year. While legacy species richness varied with fire severity (33, 32 and 26 species per plot in low, moderate and high severity plots, respectively, accounting for 84%, 82% and 68% of total pre-fire richness), it did not vary with year or with fire severity × year (Table 3). Additionally, in any given year, post-fire plots contained an average of 20 new species that were not previously found before the fire. The number of new species per plot varied with year, fire severity and their interaction (Table 3), with patterns across fire severity and time strongly paralleling patterns of total richness (data not shown).

The impacts of time since fire and fire severity on functional group richness were diverse (Table 3, Fig. 4). More short-lived forb species were found in each of the five post-fire years than were found before the fire, with the magnitude of the post-fire increase varying among fire severities and through time. The post-fire richness of long-lived forbs was similar to pre-fire richness in 2003 and 2004, the 2 yrs immediately after the fire, but then exceeded pre-fire richness in the last three post-fire years. In contrast, graminoid and woody plant richness did not differ between pre-fire and post-fire years, although some differences were observed among post-fire years.

As with total richness, total cover in upland plots varied with year and with the interaction between year

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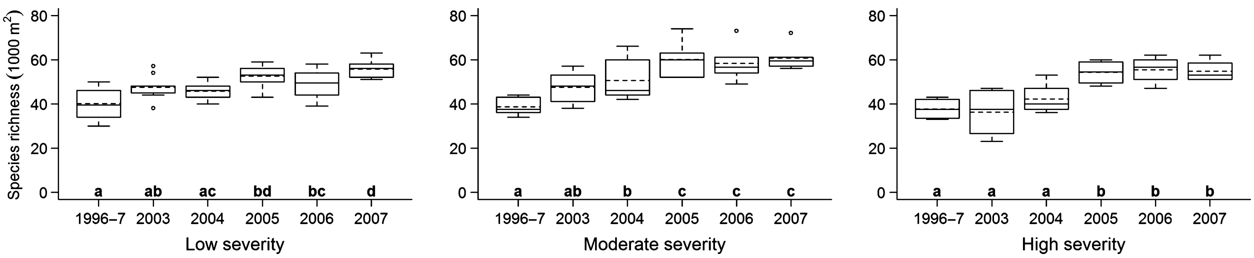

Fig. 3. Pre-fire (1996–7) and post-fire (2003–7) total species richness in upland areas burned by the Hayman Fire. Years that share letters were not significantly different at a 0.05 family-wise error rate.

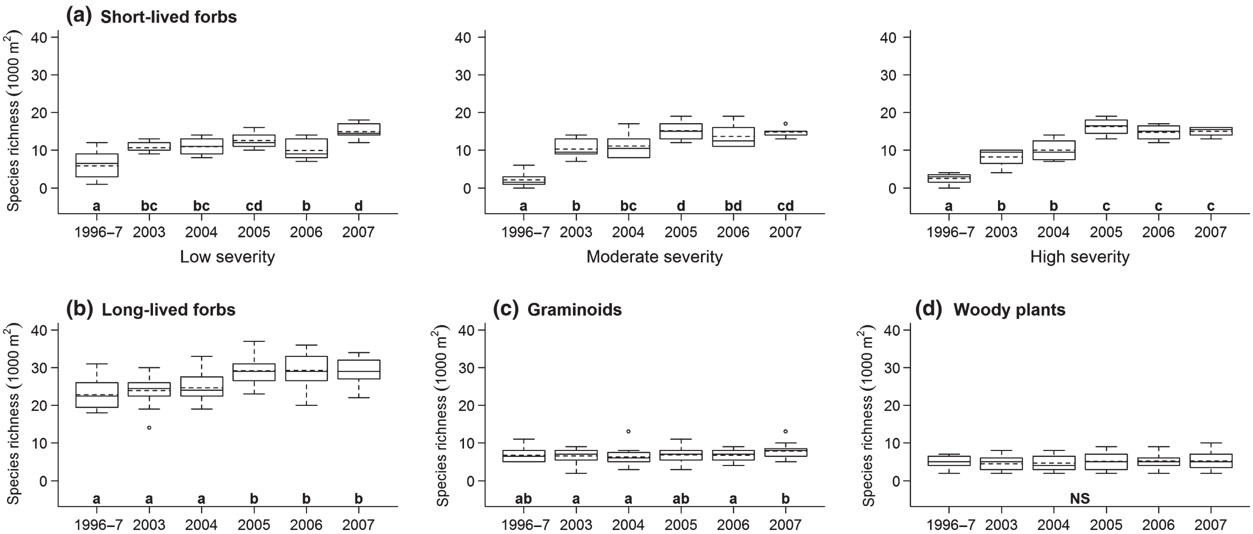

Fig. 4. Pre-fire (1996–7) and post-fire (2003–7) richness of (**a**) short-lived forbs, (**b**) long-lived forbs, (**c**) graminoids and (**d**) woody plants in upland areas. Data are shown separately for low, moderate and high fire severities only when fire severity × year was significant. Years that share letters were not significantly different at a 0.05 family-wise error rate (NS, no significant differences among years).

and fire severity, but not with fire severity *per se* (Table 3, Fig. 5). Total cover decreased initially after fire in lightly and moderately burned plots but returned to pre-fire levels by 2004 and remained there for the duration of the study. In severely burned plots, total cover also decreased initially after fire and returned to pre-fire levels from 2004 to 2006, but then exceeded pre-fire levels in 2007.

Understorey cover within all four functional groups varied with time, but only short-lived forb cover also varied with fire severity (Table 3, Fig. 6). The post-fire cover of short-lived forbs increased in lightly burned plots only in 2004, while moderately and severely burned plots saw a post-fire increase in three of the five post-fire years. Long-lived forb cover was unchanged by fire from 2003 to 2005, and then increased relative to pre-fire cover in 2006 and 2007. For graminoids, cover was lower after the fire than before for the first two post-fire years, but returned to pre-fire levels from 2005 to 2007. Woody plant cover was lower after the fire than before the fire in all post-fire years.

Compositional dynamics in burned upland forests

The NMS ordination of upland plots yielded a three-dimensional solution that explained 79% of the total variation in the understorey community data set (stress = 17.464, P = 0.004; Fig. 7). Axis 1 explained 33% of the variation alone and tended to separate plots by year, although the magnitude of the separation varied with fire severity. While low severity plots exhibited only modest separation between pre-fire and post-fire years along axis 1, indicating only modest compositional differences, in moderate and high severity plots, pre-fire and post-fire years were well separated. Furthermore, in moderate and high severity plots, earlier post-fire years (i.e. 2003 and 2004) also tended to separate along axis 1 from later post-fire years (i.e. 2006 and 2007); such a pattern was less

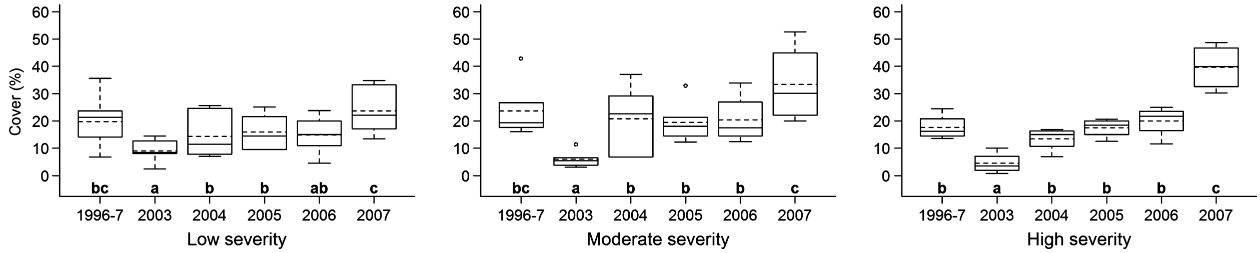

Fig. 5. Pre-fire (1996–7) and post-fire (2003–7) total species cover in upland areas burned by the Hayman Fire. Years that share letters were not significantly different at a 0.05 family-wise error rate.

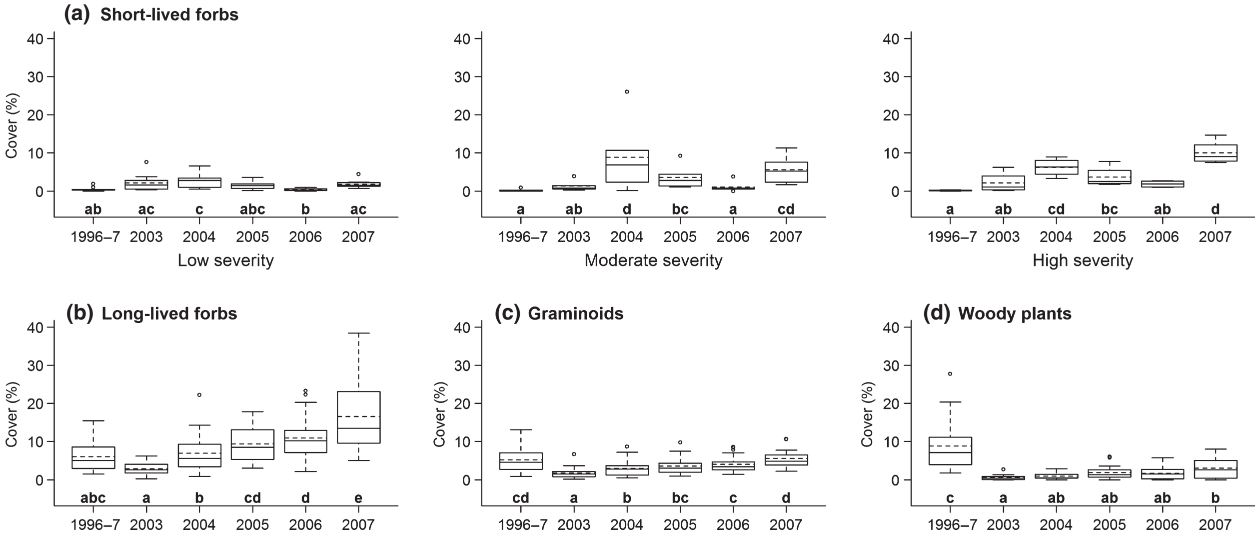

Fig. 6. Pre-fire (1996–7) and post-fire (2003–7) cover of (**a**) short-lived forbs, (**b**) long-lived forbs, (**c**) graminoids and (**d**) woody plants in upland areas. Data are shown separately for low, moderate and high fire severities only when fire severity × year was significant. Years that share letters were not significantly different at a 0.05 family-wise error rate.

apparent in the low severity ordination. Correlations between axis 1 scores and year echo these trends, as the relationship is poorer for low severity plots ($r^2 = 0.519$) than for moderate and high severity plots ($r^2 = 0.828$ and 0.797, respectively).

Post-fire understorey development in riparian forests

Total richness and cover in lightly burned riparian forests was unchanged through time ($P = 0.361$ and 0.135, respectively), averaging 78 species per plot and 37% cover across all years. Functional group richness and cover also changed little over the course of this study (Fig. 8). Differences in functional group richness were limited to short-lived forbs ($P = 0.007$); long-lived forb, graminoid and woody plant richness did not vary across years ($P = 0.658$, 0.307 and 0.858, respectively). Short-lived forb richness differed somewhat among post-fire years but did not differ before vs. after the fire. While the cover of short-lived forbs, long-lived forbs and graminoids varied among years ($P = 0.008$, <0.001 and 0.025, respectively), there were no significant pair-wise differences in short-lived forb or graminoid cover after adjustments for multiple comparisons were made, and differences in long-lived forb cover were observed only among post-fire years. Woody plant cover did not vary through time ($P = 0.103$).

Riparian understorey composition changed little over time, according to the three-dimensional NMS ordination solution that explained 93% of the variation in the understorey data set (Fig. 9; stress = 6.598, $P = 0.004$, r^2 correlation between axis one and year = 0.038). This interpretation is further supported by the fact that 81% of the pre-fire legacy species were identified in post-fire surveys in any given year (year: $P = 0.504$), and also by the fact that 46 of the 53 common riparian species were present in a similar number of plots before and after fire (Table 4). The remaining seven common riparian species, the majority of which were short-lived forbs, became more widespread following the fire for one or more post-fire years.

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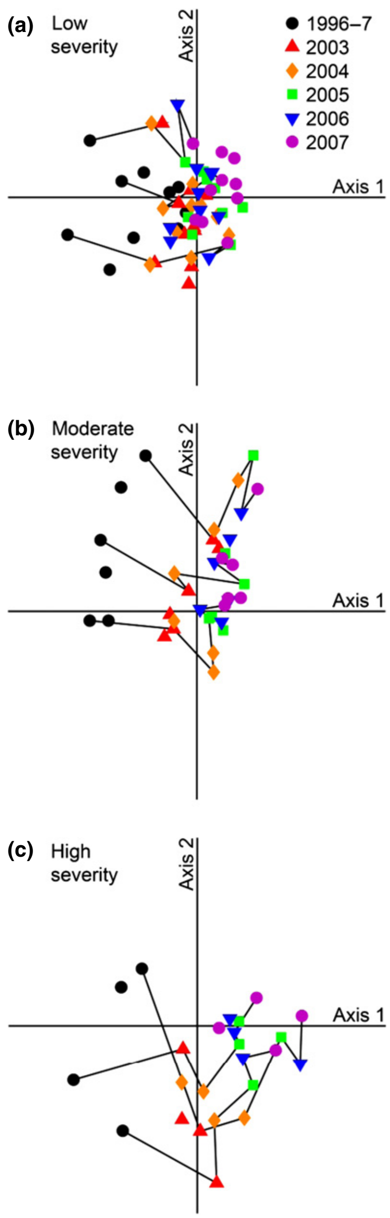

Fig. 7. NMS ordination graphs of pre-fire (1996–7) and post-fire (2003–7) understorey plant communities in (**a**) low, (**b**) moderate and (**c**) high severity upland 1000-m^2 plots. Successional vectors for three representative plots illustrate the magnitude and direction of compositional change through time.

Discussion

Understorey plant community development following fire in upland forests

A robust pre-fire and post-fire understorey data set collected within a relatively small portion of the 2002 Hayman Fire has provided a unique opportunity for examining the impacts of wildfire on understorey plant communities within upland *P. ponderosa* – *P. menziesii* forests. Across the world, the Hayman and similar megafires are commonly perceived to be ecological catastrophes (Bradstock 2008; Keane et al. 2008; Pausas et al. 2008). While the Hayman Fire may be viewed as catastrophic by some measures – e.g. by resulting in the loss of a forest cover type over extensive areas, and by threatening aquatic resources due to alterations in streamwater chemistry, sediment loads and temperature (Graham 2003; Rhoades et al. 2011) – our results suggest that it does not appear to be catastrophic from an understorey plant perspective, even in severely burned areas. Below, we support this interpretation by discussing results for the suite of upland understorey response variables evaluated here.

Of the 42 common upland understorey species we examined, over 90% of them either were present in a similar number of pre-fire and post-fire plots for each of the five post-fire years, or were present in more post-fire plots in at least 1 yr and one fire severity class. Most of the species that were just as frequently encountered before as after the fire were native long-lived forbs, graminoids and woody plants that re-established by sprouting (P. Fornwalt, pers. obs.); indeed, many of these species are known to sprout even after severe fire (Fornwalt 2009). Rapid re-establishment of pre-fire understorey species by sprouting has been found in other coniferous forests (Lyon & Stickney 1976; Anderson & Romme 1991; Wang & Kemball 2005; Laughlin & Fulé 2008), underscoring both the resiliency of these pre-fire understorey communities and their importance in shaping post-fire community composition. In contrast, species that were more frequently encountered in the years following fire were usually short-lived forbs. Post-fire increases in such species have also been observed in a variety of coniferous ecosystems (Laughlin & Fulé 2008; Bates et al. 2011). Unfortunately, several of the species that were more frequently encountered after the fire, such as *Lactuca serriola* (prickly lettuce), *Tragopogon dubius* (yellow salsify) and *Verbascum thapsus* (common mullein), are exotic. In our previous work (Fornwalt et al. 2010), we found that exotic species were especially stimulated by the Hayman Fire in severely burned areas. However, we also found that exotic richness and cover were generally low at the end of the first five post-fire years, even in severely burned areas, and correlations between native and exotic richness and cover suggested that exotics had not interfered with the development of the native understorey community.

Clearly, some common species (~10% of the species examined) were less frequently encountered following the fire, at least in one post-fire year and one fire severity class. However, these declines were largely ephemeral. Only one species, the low-growing woody plant *Arctostaphylos uva-ursi* (kinnikinnick), was negatively impacted by the fire for all

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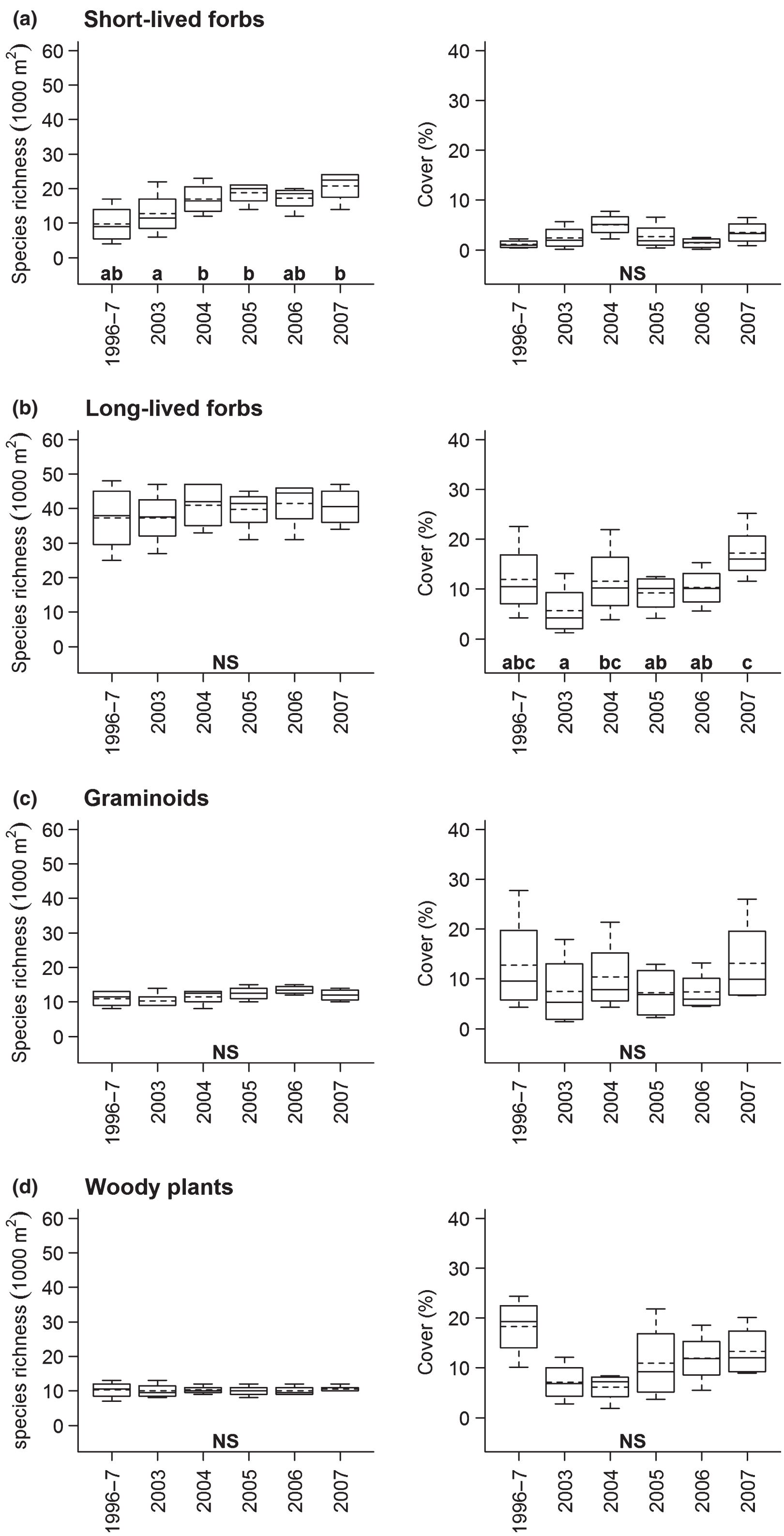

Fig. 8. Pre-fire (1996–7) and post-fire (2003–7) richness and cover of (**a**) short-lived forbs, (**b**) long-lived forbs, (**c**) graminoids and (**d**) woody plants in lightly burned riparian areas. Years that share letters were not significantly different at a 0.05 family-wise error rate.

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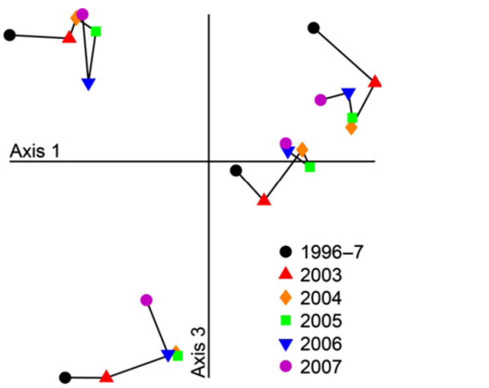

Fig. 9. NMS ordination graph of pre-fire (1996–7) and post-fire (2003–7) understorey plant communities in lightly burned riparian 1000-m^2 plots. Successional vectors illustrate the magnitude and direction of compositional change through time.

Table 4. Changes in the presence/absence of common riparian understorey species following the 2002 Hayman Fire. '–' indicates that the number of post-fire plots containing that species was similar to pre-fire values for that year, while '↑' indicates that the number of post-fire plots increased relative to pre-fire values. Common riparian species that were consistently found in a similar number of pre-fire and post-fire plots are listed after the table [a]. None of the common riparian species became less widespread following the fire.

Species	Functional Group	Response to the Hayman Fire				
		2003	2004	2005	2006	2007
Agrostis scabra	Graminoid	–	↑	↑	↑	–
Conyza canadensis	Short-lived forb	–	↑	↑	↑	↑
Corydalis aurea	Short-lived forb	↑	–	–	–	–
Elymus elymoides	Graminoid	–	–	↑	↑	–
Lactuca serriola [b]	Short-lived forb	–	–	↑	↑	↑
Laennecia schiedeana	Short-lived forb	–	–	–	–	↑
Silene scouleri	Long-lived forb	–	↑	–	↑	–

[a]Common riparian understorey species that were consistently found in a similar number of pre-fire and post-fire plots include: short-lived forbs — *Androsace septentrionalis*, *Bahia dissecta*, *Carduus nutans*[b], *Chenopodium* spp., *Phacelia heterophylla*, *Tragopogon dubius*[b] and *Verbascum thapsus*[b]; long-lived forbs — *Achillea millefolium*, *Allium cernuum*, *Antennaria parvifolia*, *Arabis fendleri*, *Artemisia ludoviciana*, *Campanula rotundifolia*, *Chamerion angustifolium*, *Cirsium arvense*[b], *Fragaria* spp., *Galium boreale*, *Geranium caespitosum*, *Heterotheca villosa*, *Linaria vulgaris*[b], *Lithospermum multiflorum*, *Maianthemum stellatum*, *Mertensia lanceolata*, *Packera fendleri*, *Penstemon glaber*, *Penstemon virens*, *Potentilla fissa*, *Pseudocymopterus montanus*, *Scutellaria brittonii*, *Solidago* spp., *Taraxacum officinale*[b] and *Thalictrum fendleri*; graminoids — *Bromus ciliatus*, *Carex* spp., *Elymus trachycaulus*, *Koeleria macrantha*, *Muhlenbergia montana*, *Poa fendleriana* and *Poa pratensis*[b]; and woody plants — *Arctostaphylos uva-ursi*, *Juniperus communis*, *Prunus virginiana*, *Ribes cereum*, *Rosa* spp., *Rubus idaeus* and *Symphoricarpos albus*.
[b]Exotic to the continental United States.

years, and only in severely burned plots. Others have also found that *A. uva-ursi* can be killed by all but the lightest of fires, and thus it is probable that 20th century fire exclusion and other land-use activities enabled this species to become more prevalent in today's forests than in historical ones (Noste & Bushey 1987; Fornwalt et al. 2009).

Understorey plant richness and cover in upland forests were dynamic in the 5 yrs following the 2002 Hayman Fire, but met or exceeded pre-fire levels by the end of this study. For all fire severities, total post-fire richness was comparable to total pre-fire richness during early post-fire years, and then increased during the last few years. This increase was primarily driven by an increase in short- and long-lived forb richness. In contrast, total cover declined in the first post-fire year for all fire severities, no doubt primarily due to the effect of the fire, but possibly also in response to the very low levels of precipitation that were observed during the year of the fire and during this first post-fire year (Keeley et al. 2005). The decline in total cover was rapidly reversed in following years as the post-fire cover of herbaceous species (i.e. short-lived forbs, long-lived forbs and graminoids) met or exceeded pre-fire levels. Both the recruitment of new species and the expansion of pre-fire species appear to be contributing to herbaceous cover dynamics in post-fire years 3 through 5. Relative to herbaceous cover, woody plant cover was much slower to recover after fire, and was still below pre-fire levels in the fifth post-fire year for all fire severities. The relatively slow recovery of woody plants is likely due to the fact that even species that vigorously sprout after fire, like *Cercocarpus montanus* (alderleaf mountain mahogany), often take many years to regain their large pre-fire size (Liang 2005), and some species, like *A. uva-ursi* mentioned above, sprout poorly after fire.

The degree of post-fire compositional change among years was highly dependent on fire severity. We found that compositional changes in lightly burned areas were modest, consistent with other observational and experimental research conducted in lightly burned *P. ponderosa* forests (Laughlin & Fulé 2008; Scudieri et al. 2010). In contrast, severe fire can cause profound and potentially long-lasting alterations in plant community composition. For example, Keyser (2007) found that understorey plant communities that burned severely in the 2000 Jasper Fire of South Dakota, USA, were converted from communities dominated by the shrub *Juniperus communis* (common juniper) to communities dominated by forbs and graminoids, largely due to the elimination of this fire-intolerant species. Although we observed compositional changes as well, results of other analyses presented here suggest that these changes were not driven by localized species extinctions; rather, they appear to be largely attributable the post-fire recruitment of new species. Furthermore, our ordination results show that compositional trajectories continued to move away from pre-fire composition as time since fire passed, coinciding with the continued accumulation of new species in these plots over the 5 yrs. While it is likely that community composition in severely burned areas will begin to move toward pre-fire conditions in upcoming years as many of the newly recruited short-lived species wane, it may take decades for understorey composition to fully return to pre-fire conditions, if at all (Halpern 1988; Savage & Mast 2005; Bataineh et al. 2006; Coop et al. 2010).

Post-fire understorey development in riparian forests

We found that post-fire understorey changes were minimal in the riparian forests studied here. This is likely due to the low severity with which they burned. After the Hayman Fire, pre-fire litter and wood lying on the forest floor was blackened or even unburned, but rarely consumed. This pre-fire material, as well as new material that continued to accumulate in the years following the fire, probably restricted the post-fire recruitment of new species (Xiong & Nilsson 1999). Some pre-fire plants also remained unburned, and most of those that did burn tended to recover readily through sprouting (P. Fornwalt, pers. obs.).

Despite the importance of riparian zones to understorey plant diversity in coniferous forests (Peet 1978; Pabst & Spies 1998; Fornwalt et al. 2009), and the importance of fire as a disturbance agent in these ecosystems (Dwire & Kauffman 2003), only a few studies have examined how riparian forest understorey communities are influenced by fire. Our results are largely consistent with their findings. For example, Arkle & Pilliod (2010) found that the cover of understorey vegetation was not impacted by a low severity prescribed fire in central Idaho. Also working in Idaho, Jackson & Sullivan (2009) found that understorey community composition in riparian forests burned by low severity wildfire was similar to that of unburned riparian zones nearby. However, they did report marked differences in community composition between unburned and severely burned riparian areas, largely due to the invasion of exotic species. Unfortunately, an insufficient number of our pre-fire riparian plots happened to fall within areas of severe fire to provide adequate sample sizes, and so we cannot speak to the influence of high severity fire on riparian areas burned by the Hayman. Clearly, more work is needed on the relationship between fire severity and understorey response in these sensitive and important ecosystems.

Conclusions

The 2002 Hayman Fire is the largest, and arguably the most severe, wildfire known to burn in Colorado to date. We found that the fire had largely neutral or stimulatory impacts on understorey plant richness and cover in upland areas, regardless of fire severity, and that changes in upland community composition were driven primarily by the post-fire recruitment of new species, rather than by a loss of pre-fire species. Post-fire understorey changes in the riparian forests we studied, which burned with low severity, were minimal.

Due to the serendipitous nature of this study, our sampling was restricted to a small portion of one wildfire. However, to our knowledge, it is the only work that documents the post-fire response of understorey plant communities in Colorado Front Range *P. ponderosa–P. menziesii* forests. Given the unnaturally high fuel loadings in these forests and the projected impacts of climate change, it is expected that fires like the Hayman will continue to occur (Litschert et al. 2012). Indeed, in 2012 the Colorado Front Range experienced one of its worst fire seasons in recorded history, with four fires alone – the Hewlett, High Park, Lower North Fork and Waldo Canyon Fires – resulting in ca. 48 000 ha burned, six people killed and 628 homes destroyed. Thus, it is essential that we continue to document post-fire vegetation development in the Hayman and elsewhere. Such research will allow scientists, managers and others to improve their ability to anticipate short- and long-term understorey recovery patterns following fire, and to determine if, when and where rehabilitation and/or restoration activities are required to meet desired conditions in burned areas.

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